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HERRERASAURIDAE, A NEW FAMILY OF TRIASSIC SAURISCHIANS

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ABSTRACT: A comparative analysis of the skeletons of the genera *Herrerasaurus* and *Staurikosaurus* is made. The results suggest that they were closely related, and shows many differences with other Triassic saurischians, principally in the pelvic girdle and hind limbs. The genera *Herrerasaurus* and *Staurikosaurus* are placed in a new family, Herrerasauridae. A definition of this new family is given. Its placement among the higher taxa of the order Saurischia is briefly discussed.

INTRODUCTION

During the recently completed revision of the Triassic saurischians of Argentina, the author suggested some conclusions of interest in reference to the systematic position of the genus *Herrerasaurus*. As is known (Reig, 1963), the genus comes from the lower levels of the Ischigualasto Formation in San Juan Province. This formation contains a varied association of tetrapods including labyrinthodonts, cynodonts, thecodonts, saurischians, ornithischians and rhynchosaurs, and can be assigned to an Ischigualastian Stage, correlated with the Carnian Stage of European chronology, and probably including the uppermost part of the Middle Triassic (Bonaparte, 1967).

The genus *Staurikosaurus*, coming from the Santa María Formation (Brazil) and described by Colbert (1970), must be included in comparisons when considering the family affinities of *Herrerasaurus*. The age of this formation, on the basis of its faunal association, is somewhat greater than that of the Ischigualasto Formation (Bonaparte,

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1966, 1970; Colbert, 1970) and possibly corresponds to the upper Ladinian or the Ladinian-Carnian boundary of European chronology.

The comparative analysis of both South American forms—known from most of their skeletons, especially the postcrania—provides clear evidence of the affinity existing between both genera, which very possibly could represent a peculiar adaptive type in the context of Triassic saurischians. On the other hand, the coexistence of certain primitive characters in *Herrerasaurus* and *Staurikosaurus* along with others revealing a marked specialization, contributes to complicating the view of their relationships. *Herrerasaurus* has been successively assigned to distinct saurischian families and included in different infraorders, as is seen in the following section. The peculiar morphological characters that this genus presents make it difficult to place it comfortably within any of the known Triassic saurischian families, and even within higher taxa.

In the present work the creation of a new family, Herrerasauridae, will be considered to include both Triassic genera, reflecting the profound differences existing with other saurischian families.

PREVIOUS OPINIONS ON THE SYSTEMATIC POSITION ASSIGNED TO *HERRERASAURUS* AND *STAURIKOSAURUS*

The genus *Herrerasaurus* (*H. ischigualastensis*) was defined by Reig in 1963 (*op. cit.*) on the basis of very well-preserved materials represented by fragmentary remains of the skull and a complete postcranial skeleton. In the cited work a diagnosis of the genus *Herrerasaurus* was given, and at the same time some of the interesting problems of the systematic and phylogenetic order that were raised were discussed.

Later there were many authors who intended to assign it a systematic position based on the Reig's brief original description and illustrations, although their conclusions generally were not founded on comparative studies.

Reig (*op. cit.*: 9) stated that "*Herrerasaurus* deserves to be attributed to the infraorder Carnosauria without much doubt; but it offers a rather confused panorama as far as its family relationships". He also carried out an evaluation of the morphology of

the pelvis, hind limb and mandibular remains, emphasizing that (p. 9) "…in certain characters it indicates having achieved the evolutionary level of *Megalosaurus*, and in others of *Antrodemus*, in spite of its great antiquity and having retained primitive features in other characters…".

Rozhdestvensky and Tatarinov (1964) cited *Herrerasaurus* as a carnosaur of the family Gryponichidae.

Walker (1964) indicated that *Herrerasaurus* was similar in many aspects to saurischians of plateosaurid type, from which it is differentiated by the presence of a foot-shaped expansion on the distal part of the pubis. Nevertheless (*op. cit.*: 107), this does not necessarily imply a narrow affinity with the Jurassic and Cretaceous carnosaurs. This author maintained that there could be some connection between *Herrerasaurus* and other Triassic forms such as that described by Case (1943) from the Dockum Formation of Texas, and *Poposaurus gracilis* Mehl 1915 from the Upper Triassic of Wyoming.

Charig *et al.* (1965: 213) indicated that some of the Triassic dinosaurs older than *Herrerasaurus* did not seem to have a satisfactory position among the existing taxa, at least until some new discoveries throw more light on the relationships existing between the four saurischian infraorders. According to these authors (p. 216), *Herrerasaurus* "…appears to exhibit a mixture of 'prosauropod' and 'carnosaur' characters".

Without prior analysis, Romer (1966) assigned *Herrerasaurus* to the infraorder Prosauropoda, and within this questionably to the family Plateosauridae.

Colbert (1970) was concerned with the systematic position of *Herrerasaurus* and *Staurikosaurus*, making comparisons between both genera. This author assigned *Herrerasaurus* to the suborder Paleopoda, which was created in 1964, and within this to the infraorder Teratosauria. The genus *Staurikosaurus* was also placed in this infraorder, although in a distinct family from *Herrerasaurus*. In effect, whereas the genus *Herrerasaurus* was assigned to the Teratosauridae, *Staurikosaurus* was classified in the family Paleosauridae.

Finally Bonaparte (1970: 673) emphasized that, although he had no doubt that *Staurikosaurus* was a saurischian, its inclusion in the Paleosauridae was questionable, and it was not impossible that this genus and probably *Herrerasaurus* represent very

primitive saurischians that do not necessarily pertain to any of the known Triassic families.

AFFINITIES BETWEEN *HERRERASAURUS* AND *STAURIKOSAURUS*

Colbert (1970) described the osteology of *Staurikosaurus pricei* in some detail and included a discussion of its affinities with *Herrerasaurus*. The conclusions to which that author arrived differ basically from the ones obtained in this work, for which reason it is advisable to make a more detailed analysis of this subject.

Staurikosaurus is represented by a partially complete skeleton, consisting of 20 presacral vertebrae, 35 caudals, the pelvic girdle, femur, tibia, fibula, both mandibular rami and the proximal part of the humerus.

It is a smaller saurischian than *Herrerasaurus*, approximately half of its size, whose bones are proportionally more gracile than those of the Argentine genus.

The cranial remains preserved are incomplete in *Staurikosaurus* as in *Herrerasaurus*, and meaningful data with respect to their affinities can be extracted from them only with difficulty. In agreement with the rest of the skeleton, the mandibular fragments of *Herrerasaurus* are more robust than in *Staurikosaurus*. In both cases, the dentition is clearly carnivorous and the size of the skull was large relative to the postcranial skeleton, as is expected in active predators. In this sense it is important to remark that both forms must have had relatively similar habits, and would have carried out comparable ecological roles in the context of the tetrapod fauna.

The vertebrae of *Staurikosaurus* are platycoelous, with widely expanded articular surfaces and deeply excavated centra. Strong crests or abutments are extended ventrally from the diapophysis in all the presacrals. The neural spines are considerably tall and anteroposteriorly short, and are slightly inclined anteriorly. The three sacral vertebrae are very massive and present wide connections with the ilium. In comparison with the vertebrae of *Herrerasaurus*, a similarity in the height and especially the anteroposterior shortness of the neural spines is evident, especially in the presacral vertebrae, which do not acquire the laminar form characteristic of prosauropod families.

The ilium of *Staurikosaurus* is a short, high blade of the "brachyiliac" type (*sensu* Colbert, 1964); the posterior spine is notably short and is prolonged ventrally, forming a wide blade; the upper border of the iliac blade is straight and suffers an abrupt inflection in the height of the anterior spine; this is short, truncated and slightly recurved laterally. The origin of the anterior iliac spine is located at the height of the deepest portion of the roof of the acetabular cavity; the pubic peduncle is wide and robust and exceeds the limit of the most anterior point of the iliac spine. Finally, the acetabular fenestra of *Staurikosaurus* is of reduced dimensions and insinuates itself as a small, half-moon-shaped entrant into the inferior edge of the ilium.

The general morphological plan of the ilium is very similar to that of *Herrerasaurus*, with which it shares important characters that are not observed in other saurischian families. The iliac blade of both genera is proportionally short and tall, although the posterior part is still more truncated in *Staurikosaurus*, as Colbert emphasized (*op. cit.*: 21). On the other hand, in both forms the acetabular cavity is deep, showing a prominent supraacetabular crest, the pubic peduncle is short, and the acetabular fenestra is of reduced dimensions. This last character is somewhat more marked in the Santa María genus, whose fenestra is more closed than in *Herrerasaurus*.

The ischium is much shorter than the pubis and is expanded in its proximal region, although its size cannot be exactly determined due to breakage. The posterior extension is slender and long, and lacks distal expansions. Compared with the ischium of *Herrerasaurus*, it has the gracility of the posterior expansion and the absence of distal expansions in common, although in *Herrerasaurus* the proximal region is wider and the contact surface with the pubis seems to have been more extensive.

The pubis of *Staurikosaurus* presents distinctive characters only comparable with those of *Herrerasaurus*. According to the description and figures given by Colbert (*op. cit.*: 14), the pubes are long and united by a distal symphysis "…forming a wide, plate-shaped structure"; the proximal region is expanded, but the form, size and position of the obturator foramen cannot be determined due to not having been completely preserved. The distal region is expanded in a "foot" that probably results (*op. cit.*: 21) from "a more general expansion of the whole inferior portion of the bone".

The pubis of *Herrerasaurus*, although it is more robust, shares with that of *Staurikosaurus* the important and disused character of the foot-shaped distal expansion. Regarding its length, the pubis of *Staurikosaurus* is somewhat shorter than the tibia, whereas that of *Herrerasaurus* is as long as the latter. As Colbert emphasized, this difference of proportions is due to the great length of the tibia in *Staurikosaurus*, a genus that very possibly was faster and more agile than *Herrerasaurus*.

The hind limb shows different proportions from *Herrerasaurus*, which are evident in the tibia/femur ratio. This index is 1.07 in the Brazilian genus and only 0.87 in the Argentine form.

The femur of *Staurikosaurus* is more gracile and the shaft more slender than that of *Herrerasaurus*; it is strongly convex anteriorly and the femoral head projects at nearly a right angle from the shaft. The fourth trochanter is situated considerably above the midpoint, at approximately 1/3 of the length from the proximal end. The location of the lesser trochanter and the fourth trochanter are very similar to *Herrerasaurus*.

The tibia also has a more slender and refined shaft than that of *Herrerasaurus*. Distally it presents a smooth expansion that barely surpasses the diameter of the shaft; the articular surface for the astragalus shows the typical step on its anterior face to receive the ascending process of this element. Aside from the greater lengthening, it has a general agreement in the morphology of the tibia. The fibula of *Staurikosaurus* is long, slender and straight, of comparable diameter to the tibia, hardly but somewhat smaller. In *Herrerasaurus* there exists a somewhat more marked disparity between the two zeugopodial elements.

Comparisons of the pes in these genera cannot be made because it has not been preserved in *Staurikosaurus*.

From the previous comparisons it may be concluded that *Herrerasaurus* and *Staurikosaurus* present a basically similar structural plan, and that the common characters that have been shown speak in favor of a familial affinity between these two genera.

On the other hand, their eventual inclusion in some of the existing families of Triassic saurischians is difficult to conceive if we rely on the peculiar features that characterize them, an aspect that will be realized in the following section.

COMPARISONS WITH THE FAMILIES OF THE INFRAORDERS PROSAUROPODA AND CARNOSAURIA

The Triassic saurischians are represented by coelurosaurs (Podokesauridae and Procompsognathidae), prosauropods (Melanorosauridae, Plateosauridae and Anchisauridae[*]) and probably carnosaurs (Teratosauridae).

Obviously the possible inclusion of the genera in question within some family of the infraorder Coelurosauria must be totally discarded, because of the clear differences that exist in the construction of the skeleton.

The assignment of *Herrerasaurus* questionably to the family Plateosauridae (Romer, *op. cit.*), and of *Staurikosaurus* to the family Paleosauridae (equivalent to Thecodontosauridae *sensu* Charig *et al.*, 1965) by Colbert (1970: 27), makes it necessary to deepen the comparisons with the families of the infraorder Prosauropoda. This group of saurischians is relatively homogeneous, and it is feasible to define them with some precision; among this morphological unity are noted only smaller differences than those which characterize each of the families, for which reason the comparisons can be carried out by taking the infraorder together.

A primary difference is encountered in the dentition, because whereas prosauropods never were definitively carnivorous forms but rather omnivores, both *Herrerasaurus* and *Staurikosaurus* were well-defined predatory carnivores. In this aspect, the conical and highly pointed teeth of these genera easily differentiate them from the spatulate or leaf-shaped teeth of prosauropod families. The aspect of feeding habit is of highest importance inasmuch as it fundamentally conditions the rest of the skeletal elements for the best fulfillment of a determined ecological role. It is thus that the vertebral column also shows explicable differences for the different size of the skull. In prosauropods it is proportionally small and the vertebral column experiences an evident lengthening by elongation of the vertebrae (fig. 1). In the family Herrerasauridae

[*] Galton (unpub.) made an analysis of the systematic position of the genus *Ammosaurus*, concluding that it was a prosauropod and not a coelurosaur, showing clear affinities with *Anchisaurus*, *Thecodontosaurus* and *Gyposaurus*. Of the three family names existing to unite these forms (Anchisauridae Marsh 1885,

(*Staurikosaurus*, *Herrerasaurus*) the size of the skull was clearly larger than in prosauropods; in agreement with this, the centrum of the more anterior vertebrae in *Herrerasaurus* (probably cervico-dorsals) and in *Staurikosaurus* (ninth presacral) is short and of approximately the same length as the rest of the vertebrae. On the other hand it is necessary to emphasize that in these genera the neural spines never acquire the laminar form seen in Prosauropoda.

The pelvic girdle is one of the most characteristic elements of prosauropod families, and its morphological plan is maintained with very small variations. As can be appreciated in Plate I (figs. 2, 3), the pelves of plateosaurids, melanorosaurids and anchisaurids clearly differ from those of *Herrerasaurus* and *Staurikosaurus* (Pl. I, figs. 5 and 6) in the proportions of the ilium and ischium, and fundamentally in the morphology of the pubis. The ilium of plateosaurids, for example, is longer due to the greater development of the spines, especially the posterior; the pre- and postacetabular pedicles are longer and more slender; the internal aperture of the acetabulum is proportionally larger. This same differences are valid for the families Melanorosauridae and Anchisauridae. Although in melanorosaurids (e.g. *Riojasaurus*) the preacetabular pedicle is shorter than in the other families (Bonaparte, 1971) and the internal aperture is more reduced, the morphological plan of the ilium of this family is entirely comparable with those of other prosauropods.

The ischia of prosauropods are more robust than in *Herrerasaurus* and *Staurikosaurus*, and almost always present a thickening of the ends of the distal projections.

Finally, the pubes of all prosauropods are of laminar type, approximately straight in lateral view and with a superficial subrectangular extension that is exposed dorsally. The pubes of *Herrerasaurus* and *Staurikosaurus* do not show characters that can be compared with those of prosauropods, except some primitive features of the proximal region such as the long suture with the ischium and the presence of well-developed pubic foramina.

Thecodontosauridae Huene 1906 and Ammosauridae Huene 1914), Anchisauridae has priority over the others.

The hind limbs of *Herrerasaurus* and *Staurikosaurus* also show significant differences with prosauropods, such that it is important to make a brief reference to this aspect. In the families Plateosauridae and Melanorosauridae, especially the latter, the appendicular bones are relatively heavy and massive. The femur is robust and the fourth trochanter is situated in about the middle third of the bone (Melanorosauridae) or in a slightly more proximal position (Plateosauridae). In contrast, the femur in the forms being considered is notably more slender (especially in *Staurikosaurus*) and the fourth trochanter is clearly situated in a more proximal position. In this last aspect the femur is somewhat more similar to those of the family Anchisauridae (Pl. II, fig. 1*b*), although the rest of the characters of this family are clearly "prosauropod".

The tibia of prosauropods shows a morphology that agrees with the robustness characterizing entire hind limb. It is proportionally short (Pl. II, fig. 2*b*) and has strongly widened proximal and distal ends, especially the former. Apart from the characters indicated, it differs from that of *Herrerasaurus* by the greater torsion between the ends. In the melanorosaurid *Riojasaurus* Bonaparte (1971) from the Los Colorados Formation, it has a moderate torsion on the order of 90°, whereas that in *Herrerasaurus* is only approximately 60°. The morphology of the distal region in *Herrerasaurus* and *Staurikosaurus* is undoubtedly of prosauropod type, with the posterior part forming a descending process and with an external depression to solidly accommodate the ascending process of the astragalus. But this region does not show the mediolateral widening seen in prosauropods, especially in Melanorosauridae and Plateosauridae.

The astragalus and calcaneum, preserved only in *Herrerasaurus*, are similar in general aspect to those of the prosauropod families.

Finally, the pes (preserved complete in *Herrerasaurus*, except for some phalanges) (Pl. II, fig. 3) also shows clear differences with those of prosauropods, especially with Plateosauridae and Melanorosauridae, and to a somewhat lesser degree with Anchisauridae (Pl. II, fig. 3). In *Herrerasaurus* the metatarsals are characterized by their length and gracility, as are the phalanges. On the other hand, it is symmetrical relative to digit III, not displaying the marked reduction of metatarsal V seen in prosauropods. Another peculiar character that the pes of this genus possesses is the

marked reduction in width of metatarsals I and V, whose diameter is only a little greater than half that of the three central metatarsals.

On the basis of these comparisons, it is considered that clear differences are given between *Herrerasaurus* and *Staurikosaurus* and the three prosauropod families. Because of this, I believe that it is not reasonable to assign these genera to any of the families of the infraorder Prosauropoda. It seems clear that the adaptive type represented by both South American forms—very possibly permanently bipedal and carnivorous—differs substantially from that which the prosauropods must have possessed.

Their possible inclusion among some family of the infraorder Carnosauria must also be thoroughly considered. Lamentably, this infraorder is poorly represented during the Triassic, as opposed to the excellent record it has in the Jurassic and Cretaceous. For this reason comparative elements are few and often hardly conclusive for specifying affinities. The question of the named "Triassic carnosaurs" was recently highly debated (Walker, 1964; Colbert, 1964; Charig *et al.*, 1965; Bonaparte, 1969), although it still constitutes one of the less clear aspects of the phylogeny and classification of the order Saurischia.

The classically known families of Triassic carnosaurs were Paleosauridae (including Gryponichidae) and Teratosauridae. The first, as Romer already emphasized (1956: 514), is difficult to separate from primitive prosauropods such as *Thecodontosaurus*. Charig *et al.* (*op. cit.*) emphasized that the classification of forms such as *Gryponix* among the carnosaurs was based only on certain similarities between their forelimb and those of some Jurassic carnosaurs. Since there exist no differences in the postcranial skeleton, they assimilate the family Gryponichidae into Thecodontosauridae (Anchisauridae *sensu* Galton, unpub.), a criterion that seems very reasonable in light of recent evidence.

The family Teratosauridae is composed of the genera *Teratosaurus* and *Sinosaurus*, the first from the Upper Triassic of Germany (Stubensandstein) and the second from the Upper Triassic of China (Lufeng Series). Both genera are represented by cranial remains of definitively carnivorous type and postcranial skeletons of prosauropod type. Nevertheless, the association of these remains is not supported by conclusive evidence, as Charig *et al.* (*op. cit.*) remarked. These authors chose to assign

the postcranial remains to the infraorder Prosauropoda, because of the impossibility of differentiating them from the limbs of this saurischian group, whereas the cranial remains are maintained in the family Teratosauridae. Subsequently this family is included in the infraorder Carnosauria (Charig *et al.*, 1967) in the superfamily Tyrannosauroidea.

Walker (1964: 107) came to the same conclusion as the preceding authors and admitted that the only remains that could be reasonably assigned to true carnosaurs are the cranial fragments of *Teratosaurus* and *Sinosaurus*. The remaining material of Plateosauridae and Teratosauridae is placed provisionally among the prosauropods. Both genera are grouped with *Ornithosuchus* in the family Ornithosuchidae, within the infraorder Carnosauria.

Colbert (1964: 18) restricted the term "carnosaur" to the large Jurassic and Cretaceous carnivores, creating the new infraordinal group "Teratosauria" to include the Triassic carnivorous forms, which according to this author were separated phylogenetically from the "true carnosaurs", that is the megalosaurids and tyrannosaurids. This infraorder, to be included with Plateosauria* in the suborder Paleopoda, presents characters basically similar to those used to define prosauropods, particularly those referring to the postcranial skeleton. According to this author, the differences are fundamentally in the size of the skull and the type of teeth, characterizing, according to the original text (*op. cit.*: 20), "small to rather large paleopods, skull varying from moderate to large size with sharp teeth. Astragalus and calcaneum closely appressed to tibia and fibula". It is clear that the inclusion of the family Teratosauridae in the infraorder Teratosauria thus defined admits, in principle, the association of the cranial and postcranial remains. For that reason, the differences between *Herrerasaurus* and the family Teratosauridae are the same as has already been noted for the infraorder Prosauropoda.

In contrast, if it is accepted that the family Teratosauridae is defined on the basis of the cranial remains (Charig *et al.*, Walker), the supposed similarities in the dentition do not constitute in a single case a solid argument for uniting them in the same family. In my opinion, there does not even exist significant evidence that permits deciding whether

the cranial remains of *Teratosaurus* truly pertain to a carnosaur or to a carnivorous thecodont. In this aspect it is noticed that a marked similarity exists between the maxilla figured by von Huene (1908, Pl. 64, fig. 1) and the maxillae of certain rauisuchid thecodonts such as *Sarcosuchus* Reig (1961), both in the morphology of the dentary and in the disposition of the interdental plates.

On the other hand, the inclusion of *Staurikosaurus* in the family Paleosauridae (Colbert, 1970) is also doubtful due to the clear differences existing between the pelvis of *Paleosaurus* and that of the Brazilian genus; neither the size of the skull nor the nature of the teeth indicate affinities with this family, which shows clear "prosauropod" characters.

From the analysis that was made, I consider that the conclusion arises that *Herrerasaurus* and *Staurikosaurus* cannot be assigned to any existing saurischian family. Because of this I propose creating a new family, Herrerasauridae, to include both South American genera, which can be defined as follows.

HERRERASAURIDAE, Nov. Fam.

DIAGNOSIS:

Saurischians of carnivorous habits, moderate size and bipedal posture. Presacral vertebrae tall, with anteroposteriorly short neural spines; ilium shorter than in Prosauropoda, tall, with anterior spine short and posterior spine truncated or rounded. Acetabular cavity strongly excavated and supraacetabular crest prominent; acetabulum with incipient aperture. Pubis proportionally long, with development of a distal "foot", expanded sagittally and laterally compressed. Ischium much shorter than the pubis, with slender distal elongation, without expansion. Sacrum with three vertebrae. Femur sigmoid, slender, with the fourth trochanter situated above the midshaft. Slender tibia, with little torsion between its ends, little expanded distally and with descending posterior process. Astragalus and calcaneum of prosauropod type, the former strongly connected to the tibia. Pes with elongate metatarsals, symmetrical around digit III; metatarsals I and V narrower than the others, but longer and of approximately the same length; elongate phalanges. Forelimb with tendency toward reduction.

Family *HERRERASAURIDAE*

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[*] Colbert (1964) included the families Melanorosauridae, Plateosauridae and Thecodontosauridae in the infraorder Plateosauria, for which reason this saurischian group would be equivalent to the infraorder Prosauropoda of the remaining authors.

Herrerasaurus ischigualastensis Reig, 1963
Staurikosaurus pricei Colbert, 1970

CONCLUSIONS

In the author's opinion, the grouping of *Herrerasaurus* and *Staurikosaurus* within a new family constitutes a first step toward facilitating the systematic placement of these genera. Nevertheless it still remains to establish the possible phylogenetic relationships of the family Herrerasauridae with the other families of Triassic saurischians, as well as the role that it could have played in the origin of "true carnosaurs". The clarification of these fundamental aspects depends on the placement of the family Herrerasauridae among higher taxa.

In principle the placement of this new family within the suborder Sauropodomorpha (according to the classification of Charig *et al., op. cit.*) seems highly improbable if we rely on the profound differences that have been noted with respect to prosauropods. The existence of certain common characters among them, principally the similarity in the tibia-astragalus relationship, it is explicable if one considers that, at the level of current knowledge, the herrerasaurids as much as the prosauropods represent primitive forms of saurischians that originated from a relatively close common ancestor. In this stock of saurischians we have a first stage in the development of digitigrady, when the astragalus and calcaneum had already been substantially modified from the thecodont condition (see Bonaparte, 1969), but still had not developed the specialization of post-Triassic forms and even of some Triassic coelurosaurs (e.g. *Syntarsus* Raath, 1969). This stage was common to melanorosaurids, anchisaurids, plateosaurids and herrerasaurids; but in this latter certain specializations developed from the carnivorous and bipedal forms, such as the distal expansion of the pubis (probably related to a greater development of the hind limb musculature), shortening of the neck, elongation of the pes, etc., which clearly differentiated them from other Triassic forms.

Since they are carnivorous forms, is it possible to place them among the theropods? If we base this exclusively on their feeding habit it would be allowable to include the family Herrerasauridae among the carnosaurs. But the definitions that have been given for this infraorder are based principally on the Jurassic and Cretaceous forms, which represent a much more advanced evolutionary grade. As a result, the characters that define this infraorder (morphology of the pelvic girdle, number of sacral vertebrae, tibia-astragalus relationship, morphology of the pes, etc.) do not allow introducing forms such as *Herrerasaurus* and *Staurikosaurus* unless this saurischian group is redefined. Perhaps a more correctly guessed alternative would be to create a new infraordinal group within the theropod lineage.

The detailed restudy of the osteology of *Herrerasaurus* that the author is carrying out will possibly contribute new elements for judging the phylogenetic relationships of this family. It is possible to anticipate that it will make re-framing the present classification schemes more likely, in order to contemplate the placement of these particular Triassic saurischians.

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FIGURE CAPTIONS

Fig. 1. — **A**: Cervical vertebra (8th) of ***Riojasaurus incertus*** (Melanorosauridae) (from Bonaparte, 1971); **B**: Cervical vertebra (9th) of ***Staurikosaurus pricei*** (from Colbert, 1970); **C**: "Cervico-dorsal" or last cervical vertebra of ***Herrerasaurus ischigualastensis*** (drawn by the author). (Not to scale.)

PLATE II.

Pelves of thecodonts and saurischians. (Not to scale.) **1**. ***Coelophysis*** (from Raath, 1969); **2**. ***Paleosaurus*** (from Colbert, 1964); **3**. ***Plateosaurus*** (from Galton, unpub.); **4**. ***Ornithosuchus*** (from Walker, 1964); **5**. ***Herrerasaurus*** (from Reig, 1963, modified. The dotted line indicates the probable original torsion of the pubis); **6**. ***Staurikosaurus*** (from Colbert, 1970).

Comparative scheme of the femur (fig. 1), tibia (fig. 2) and pes (fig. 3) in ornithosuchid thecodonts and Triassic saurischians. **1**: Femur, ventral view. **1A**: ***Riojasuchus tenuisceps*** (from Bonaparte, 1971); **1B**: ***Gyposaurus sinensis*** (from Young, 1940); **1C**: ***Riojasaurus incertus*** (from Bonaparte, 1971); **1D**: ***Herrerasaurus ischigualastensis*** (from Reig, 1963); **1E**: ***Staurikosaurus pricei*** (from Colbert, 1970). **2**: Tibia, lateral view. **2A**: ***Riojasuchus tenuisceps***; **2B**: ***Riojasaurus incertus***; **2C**: ***Herrerasaurus ischigualastensis***; **2D**: ***Staurikosaurus pricei***. **3**: Right pes. **3A**: ***Riojasuchus tenuisceps***; **3B**: ***Riojasaurus incertus***; **3C**: ***Ammosaurus major*** (from Marsh, 1896); **3D**: ***Herrerasaurus ischigualastensis***. (Not to scale.)